Mycorrhiza of Forest Trees

By V. SLANKIS[1]

THE SIGNIFICANCE of mycorrhizal fungi as a persistent component of the forest soil microflora and the importance of these fungi in tree growth can no longer be denied. Hundreds of scientific papers have been published, and many comprehensive reviews (5, 6, 10, 11, 13, 23, 24, 29, 33, 50, 60) have considered the findings reported in these publications. This paper reviews, briefly, the general morphological and anatomical characteristics of mycorrhizal roots and the role of these organs in supplying nutrients to the tree. It does not cover at length specific experiments that have been undertaken at the Forest Biology Laboratory, Maple, or elsewhere. The main emphasis will be placed on the causality of morphogenesis of mycorrhizal roots, the influence of the lower symbiont on the development of the entire root system, and some of the principles that underlie the initiation and establishment of the mycorrhizal association. It will also draw attention to a number of important areas into which future research might well be directed.

Mycotrophy or symbiosis between higher plants and certain fungi is a common phenomenon in the plant kingdom. Up to 80 percent of plants are believed to be in symbiotic relationship with certain species of fungi. Particularly among forest trees, mycotrophy is widespread and even habitual. A close examination of fragments of root systems of normally developed forest trees reveals that a large number of feeding roots, or short roots, possess a peculiar morphology. These roots are swollen, often richly branched, lacking root hairs and, as a rule, they are surrounded by a thick hyphal sheath. When sections of these roots are examined under the microscope it is seen that hyphae are present in the outer layers of the cortex but never in the central cylinder or meristem. The peculiar morphology and the presence of hyphae in a definite pattern in the cortical cells indicate that we are dealing with mycorrhizae, literally "fungus-roots", specific organs which differ in many respects from non-mycorrhizal roots.

Based on the interrelationship that exists between the root cells and fungous hyphae, forest tree mycorrhizae are classified into two main types: *ectotrophic* and *endotrophic*. The majority of the forest trees thus far investigated have ectotrophic mycorrhizae. Ectotrophic mycorrhizae are formed mainly by higher fungi belonging to the Hymenomycetes and Gasteromycetes. In this type of mycorrhizae the surface of the root is covered with a compact hyphal mantle which isolates the root from direct contact with the soil. Concurrently, the hyphae of the fungal symbiont have penetrated the outer layers of the cortex and surrounded the cortical cells as a dense net, called the "Hartig net". Because of this net, the cells are separated from each other by mycelial partitions. Endotrophic mycorrhizae are formed by lower, Phycomycetous fungi and only a few tree species form this type of mycorrhizal association.

In endotrophic mycorrhizae, the hyphae of the lower symbiont are found in the cortex, mainly intracellularly, as coils, swellings or minute branches, where they are confined within certain limits by the digestion activity of the cells. On the surface of these roots, only individual hyphae appear at the point where they enter the roots from the soil. Between these two types of mycorrhizae intermediate forms are found. In certain soils unfavorable for tree growth and mycorrhizal formation, often the roots are invaded by parasitic fungi and so-called *pseudomycorrhizae* are formed. Although the gross morphology of the false mycorrhizae is somewhat similar to that of ectotrophic mycorrhizae, the hyphae of the fungus are not restricted to certain tissues and the invasion of the cells often results in their destruction.

Our present knowledge about mycotrophy of forest trees concerns mainly ectotrophic mycorrhiza, since this type of symbiosis has received most attention. Very little, on the contrary, is known about endotrophic mycorrhiza; in particular, the physiological relationships between the two symbionts in this association are far from clear. Modern studies of mycorrhizal symbiosis date from 1885 when Frank (17, 18) in Germany published two papers on tree mycorrhiza. In these papers he postulated that the water and nutrients that enter the tree through mycorrhizal roots are obtained from the fungal symbiont. This postulation aroused a torrent of contradictory opinions.

Several distinguished contemporary botanists labeled mycorrhiza an association without any significance for the tree or even declared that the fungus is a harmful parasite. However, research carried out

[1]Forest Biology Laboratory, Science Service, Canada Department of Agriculture, Maple, Ontario.

on mycorrhizal symbiosis, particularly during the last three decades, has provided evidence that especially in poor soils this association is beneficial to the tree, and that under certain conditions mycorrhiza is even necessary for normal tree development. The beneficial effect of this symbiosis has been convincingly demonstrated in different parts of the world – West Australia (34, 93), Philippines (65), South Africa (3), Java and Sumatra (69), North America (28, 59, 92) and others – where attempts to afforest forestless areas failed because of the lack of mycorrhizal fungi in the soil. However, as soon as the soil was inoculated with pure cultures of known mycorrhiza-producing fungi or with soil taken from an old forest stand, afforestation was successfully accomplished.

Similar inoculation trials were made in Russia in order to afforest steppes with oak (89). Recently in the United States, inoculation of prairie soil with mycorrhizal fungi produced a beneficial effect on poplar cuttings. Preliminary results show that the growth of inoculated cuttings was better and their survival was approximately 14 percent higher (4).

It has been possible, using radioactive isotopes, to provide an explanation for the beneficial effect of mycorrhizae. Experimental evidence was obtained that these structures function as nutrient-absorbing organs; through the hyphae of the lower symbiont, inorganic as well as organic nutrients are absorbed from the soil and translocated into the roots of the host plant (25, 26, 35, 36, 53, 54, 55, 56, 57, 58). Furthermore, it is evident that in comparison with non-mycorrhizal roots, mycorrhizal roots are more efficient nutrient absorbing organs. The more efficient nutrient uptake through mycorrhizae is reported by several research workers (35, 61, 93). Extremely interesting in this connection are data published by Hatch (28) in the United States, which demonstrate that white pine seedlings cultivated in prairie soil and inoculated with mycorrhiza-forming fungi contained 86 percent more nitrogen, 230 percent more phosphorus and 75 percent more potassium than plants without mycorrhizae. This increased efficiency results from considerably larger absorbing surfaces due to the swellings and branching of these roots, the hyphal mantle surrounding them, and the extensive hyphal net-work continuing from the mantle and ramifying into the soil (29). In addition, the hyphae of the fungal symbiont are capable of competing more effectively than roots alone with other soil microorganisms for available nutrients.

Studies on the causality of morphogenesis of mycorrhizal roots have revealed that the role which the fungus plays for the benefit of the tree in mycorrhizal symbiosis is much broader than had been suspected. Besides the nutrient supply from the soil the fungus provides the host plant with its own exuded metabolites (38, 74). Based on data obtained from experiments in which synthetic auxins such as indoleacetic acid, indolebutyric acid and others were used (75, 76, 77), it can be concluded that one of the constituents in the fungus-exuded metabolites is related to auxins, presumably indoleacetic acid, since several microorganisms are known to exude this compound as a metabolic byproduct (84). Furthermore, from these experiments it can be concluded that fungous auxin when translocated into the invaded roots plays a multifarious role in the host plant. Under the influence of this auxin, the invaded roots undergo morphological changes characteristic of ectotrophic mycorrhizae such as swelling and branching and thus it becomes evident that this fungus metabolite is responsible for the increased absorbing surface of these roots (77, 78, 79).

The important role which auxin plays in plant metabolism is well known (73, 84). The extreme changes in the morphogenesis of mycorrhizal roots, particularly the swellings resulting from cortical cell hypertrophy, which seem to be a prerequisite for the establishment and functioning of the symbiotic relationship, suggest that this fungus auxin has induced profound changes in the metabolism of these roots. Recently, studies on root metabolism in which labeled C^{14} was used have demonstrated that the biochemical activity of the roots plays a significant part in the general metabolism of the plant. It has been shown that, during definite periods in life of the plants, up to 50 percent of the assimilates, chiefly sucrose, are directed from the leaves to the roots. Organic acids and amino acids make up an insignificant part of the downward flow. In the roots, sugars are rapidly converted into ionic compounds, among which organic acids are predominant; later amino acids and ureides are formed (37).

In view of the few indications already obtained that there are differences in the metabolism of mycorrhizal and non-mycorrhizal roots (35, 67, 71) it would be of vital importance to know the nature of the metabolic changes in the cells of mycorrhizal roots induced by the fungus auxin. Since, for the formation of mycorrhizae, this auxin-like metabolite of the fungus seems to be required at concentrations far exceeding the limit of its physiological action in plants (22), the changes in cell metabolism must be considerable.

The influence of mycorrhizal infection on the development of the root system has been frequently discussed, and several opinions have been expressed. According to an early concept, any of the lateral roots, if infected by mycorrhizal fungi at their initial stage, are inhibited in their elongation and so become mycorrhizal short roots. Because of this inhibited growth,

the total surface of the root system is reduced. Later, it was suggested that lateral roots differ in their vigor or in their physiological state. The growth of only feeble laterals becomes inhibited if the infection is strong enough (1).

Recently, still another theory has been presented by Hatch (29). According to this theory, new laterals are predestined to develop into short or long roots by the fertility of the soil. It was demonstrated, experimentally, that as the nitrogen content of the soil increases, the short/long root ratio decreases. In Hatch's opinion, the growth of the predestined long roots cannot be inhibited by fungus infection, but infection of predestined short roots results in an enlargement of the root surface due to the morphogenesis which every short root undergoes during its conversion into mycorrhiza. Thus, contrary to the earlier opinion, mycorrhizal infection does not result in a decrease but in an increase of the total surface of the root system.

However, recent experiments using synthetic auxins to study the influence of fungus exuded auxin on root system development, have provided evidence that fungus auxin exerts a stronger influence than soil fertility on the development of lateral roots of pine. With an increasing concentration of auxin, externally applied, the elongation growth of long roots and new lateral roots is increasingly arrested and the majority of these new laterals become short roots. At relatively high concentrations all new laterals become extremely swollen short roots (77, 78, 79). From these results we may theorize that the growth of any lateral root, though this root may be, as Hatch has stated, predestined physiologically by soil fertility to become a long root, is inhibited by mycorrhizal infection if the fungus is able to translocate auxin at a reasonably high concentration into the root.

Naturally, it can be questioned if the influence of fungus auxin is confined to the mycorrhizal roots or if at least a part of it is translocated into the long roots so that the whole root system comes under its influence. Examination of root systems of pine and spruce under natural conditions has revealed several interesting characteristics in root system development related to the mycorrhizal association: 1) The distal parts of the long roots bearing mycorrhizae in large numbers are often swollen over a relatively long distance. Sometimes, near the swollen apex of these long roots, an increased number of short roots are initiated. These short roots are already swollen as they emerge from the epidermis. 2) Occasionally colonies of newly-developed mycorrhizal roots are formed on the proximal and middle parts of the old long roots. 3) On occasion, new mycorrhizal roots develop in the axils of old short roots as well as old mycorrhizal roots. That it is possible to reproduce similar morphological formations under laboratory conditions, by applying auxin at certain concentrations externally to the whole root system, is already known (77, 79).

Recently, however, studies on the translocation of auxin in pine roots have revealed that a similar morphogenesis is induced by synthetic auxin which when applied to one part of the root system is absorbed and translocated into the rest of the root system (81). It was found that there is a close correlation between the auxin concentration in the roots and the development of short and long roots. Relatively low auxin concentrations in the long roots stimulate elongation of these roots and also the elongation of the newly developed laterals. In this way more long roots are produced. On the contrary, relatively high auxin concentrations in long roots bring about an inhibition of long root elongation. This inhibition results in a swelling of the distal part of the long roots followed by the initiation of new short laterals in increased numbers. These results may provide an explanation for the interesting data reported by McComb (46, 47) to show that conifer seedlings with mycorrhizae obtained from nursery beds where this symbiosis was developed spontaneously in local patches, had twice as many short roots as seedlings without mycorrhizae, and that only half of them were mycorrhizal.

These experimental results give us reason to presume that the influence of mycorrhizal infection on the root system reaches beyond the rootlets with which the fungus associates. Fungus auxin, translocated into the long roots, determines broadly the sequence and frequency of long and short roots, that is, the pattern and the total surface of the root system. Direct fungal infection in new laterals also determines, to a certain degree, the fate of physiologically predestined long roots which, through inhibition of elongation, may become short roots.

Some investigators have reported that the Hartig net is present also in long roots bearing mycorrhizae (15.68). Data published by Robertson (68) indicate that there is a close relationship between the development of the Hartig net in the long roots and the formation of mycorrhizae. These data are of extreme interest in their suggestion that fungus infection profoundly influences the development of the root system. It appears, then, that the early concept of the influence of mycorrhizal infection on the root system requires some revision.

There is a possibility that fungus-produced auxin is translocated even beyond the root system, so that the aerial parts of the host plant also are brought under its direct influence. Investigations in this sphere would be of great interest.

Although we know in forest biology that trees are

nourished with the aid of mycorrhiza, research on this symbiosis has been in a very subordinate position for many years. For many practicing silviculturists, mycorrhiza is still an undefined word. To be sure, we lack a great deal of information about the mechanism under which this symbiosis functions; particularly the metabolic relationship between both symbionts is far from clear. For this reason, we are far from being able, under natural conditions, to harness this symbiosis for the maximum benefit of trees. On the contrary, we have to acknowledge the intensive research carried out on another symbiosis which is important in agriculture, that is, the symbiosis between the nitrogen fixing symbiont, *Rhizobium*, and leguminous plants. As a result, the knowledge of this symbiosis and its practical application is more advanced.

Continuous intensive research on forest tree mycorrhiza has been carried out only in a few European countries. In this connection England should be mentioned, and particularly Sweden, where Melin is the outstanding investigator in this field. In America, although initiated on several occasions, mycorrhizal research was always discontinued after a short period of activity. Recently, however, the importance of mycorrhizal symbiosis in forestry has received increased recognition, especially in those countries that have an important forest economy. In Canada and the United States this field of research has been incorporated as a permanent part in the governmental program for scientific development. Most promising is the action of the International Union of Forest Research Organizations by which, in 1957, a working group on mycorrhizal research was formed. It is intended that this group, with members from different countries, should promote the exchange of information, methods, and results of experiments. These developments encourage us to hope that the growth of our knowledge of mycorrhizal symbiosis in forest trees and its application in forestry practice will be greatly accelerated in the immediate future.

To reach our goal, intensive applied and basic research on mycorrhizal symbiosis should be carried out concurrently. On one hand, research should be directed mainly towards finding solutions to the problems which are of prime importance in nursery and plantation practices. It would be of great importance to produce, in forest nurseries, seedlings with well developed mycorrhizae. From the data obtained through basic research we know that high light intensity, adequate pH of the soil, good aeration, moderate soil fertility and humus, are the factors which stimulate the formation of mycorrhizae (13, 33, 50).

In addition, attention should be paid to the inoculation of nursery soil with selected mycorrhizal fungi. In order to gain the maximum benefit from mycorrhizal symbosis, seedlings should be associated with the fungi which are best suited to specific tree species and which are best able to tolerate those particular environmental conditions which exist in the plantation site. Association with an unsuitable mycorrhiza-former can be even detrimental to host plant development (40).

In agriculture the selection of efficient and suitable *Rhizobium* strains has resulted in a considerable increase in crop production of leguminous plants. Undoubtedly, the selection of mycorrhizal fungi suitable for specific environmental conditions would afford wide possibilities in afforestation of sites where the growth conditions for normal seedling development are most unfavorable. Of great interest in this connection are experiments recently carried out in Austria in an attempt to afforest with spruce certain mountain regions at an altitude up to 2200 meters (63).

Promising results were obtained when the spruce seedlings were inoculated with selected mycorrhizal fungi which were able to resist these extreme climatic conditions. In the Pacific Northern Forest and Range Experimental Station in the United States, an effort is being made to select xerophytic and heat-resistant mycorrhizal fungi to be used in afforestation on sites where drought and high soil temperatures prevail (86). Related to the selection of proper mycorrhizal fungi is the necessity to find suitable methods for mass production of these fungi in pure cultures. Some attempts to solve this problem have already been made in Russia (6).

However, we must keep in mind that in order to establish control of this symbiosis and obtain its maximum benefit for the tree, basic research must go hand in hand with applied research. There are still many problems to be solved in studies of the physiology of the mycorrhizal relationship, particularly those problems related to the mechanism of the initiation and the establishment of symbiosis. According to Björkman's "Carbohydrate theory", the determining factor for the establishment of mycorrhizal relationship is a surplus of soluble sugars in the roots (8, 9). Since mycorrhizal fungi, as a rule, are unable to utilize high molecular carbohydrates, such as cellulose and lignin (32, 41, 42, 48, 49, 64), the theory claims that the fungus, seeking soluble sugars, enters the roots only if an excess of these sugars is present in the roots. Further, according to this theory, the surplus of soluble sugars in the roots is secured if a certain, not too great, deficiency of easily available nitrogen or phosphorus in the soil is combined with a high light intensity available for photosynthesis. At a low light intensity, for instance at 6 per cent of full daylight, no mycorrhizae are formed.

The close relationship between the formation of mycorrhizae and the light intensity has been confirmed by other investigators (27, 90). Recently, however, experimental data obtained under laboratory conditions indicate that the mechanism of the establishment of the mycorrhizal relationship is exceedingly complicated. Thus, intact roots of white pine seedlings cultivated in nutrient solutions containing synthetic auxins in relatively high concentrations and soluble sugars do not undergo the morphogenesis characteristic of mycorrhizal roots if the seedlings are cultivated at a low light intensity (80).

Since roots readily absorb soluble sugars such as glucose and fructose from solutions it would be wrong in this case to assume that the reason for the inactivity of the auxins is some deficiency of soluble sugars in the roots. Presuming that the profound morphological changes induced by the fungus during the conversion of roots into mycorrhizae is a prerequisite for the establishment of the symbiotic relationship, then, from the data obtained experimentally with synthetic auxins, we must conclude that the establishment of symbiosis is based on an extremely complicated metabolic relationship between the mycorrhiza-producing fungus and the root. These data confirm that this relationship is not determined only by a surplus of soluble sugar in the roots. The presence or absence of some other metabolite in the roots may be of equal importance.

Even less is known about the factors which determine the initial stages of mycorrhizal development. The principles governing the entrance of the hyphae of the fungal symbiont into the roots are far from clear. In the case of ectrophic mycorrhiza this entry is gained by means of pectolytic enzymes with which the fungus dissolves the middle lamellae of the cortical cells. Pectolytic enzymes are produced by many other soil inhabiting fungi. However, under conditions favorable for mycorrhizal formation, the non-mycorrhizal fungi, including a number of efficient pathogens, are unable, as a rule, to enter the roots. Furthermore, it must be admitted that under certain environmental conditions, such as in soils of high fertility, even the hyphae of mycorrhizal fungi do not invade the roots (8, 29, 61).

Intensive agricultural studies carried out during the last 30 years on the rhizosphere have provided evidence that the exudates of the roots exert a strong influence upon the activity of soil microorganisms and largely determine the constitution of the rhizosphere population. These exudates simultaneously stimulate certain microorganisms and depress others. There is a possibility that, under conditions adequate for mycorrhizal formation, the roots exude antibiotics which have an inhibiting influence on pathogens and trivial fungi. Very interesting in this connection are data reported by Timonin (85), that root exudates of a variety of flax susceptible to *Fusarium* wilt stimulate the growth of *Fusarium* and *Helminthosporium*, whereas the root exudates of a resistant variety of flax have a depressing influence upon both fungi. This is due to the presence of hydrocyanic acid in the exudates. The same root metabolite, however, stimulates the growth of *Trichoderma*. Furthermore, it is well known that those roots of agricultural plants that have been investigated exude amino acids, sugars, vitamins, and other organic compounds (2, 7, 12, 16, 19, 20, 21, 30, 31, 44, 45, 91) which exert a growth promoting influence upon the rhizosphere-inhabiting microflora. In regard to mycorrhizal fungi, it is evident that these soil inhabitants are particularly dependent upon the root metabolites of the host plant and are able to produce fruiting bodies only when in association with tree roots (70).

Extensive nutritional studies, carried out under laboratory conditions by Melin and his students, have provided evidence that, in general, mycorrhizal fungi are unable to utilize high molecular carbohydrates such as cellulose and lignin, and that many of these fungi are partially or totally unable to synthesize some vitamins, amino acids and other still unidentified growth substances (50, 51). It is manifest that in order to accomplish its full life cycle the fungus must obtain several of these vital substances from the tree roots.

It has been found that roots produce at least one metabolite which greatly stimulates the growth of the fungal associate (52). However, this factor, called the "M-factor", is not yet identified. Recently, studies carried out on root exudates of tree seedlings using radioactive isotopes have shown that nine-month old seedlings of white pine, with their needles exposed to labelled carbon dioxide for eight days, exuded more than 35 different radioactive organic compounds (82). Among these exuded metabolites, several sugars, amino acids and organic acids were found. However, most of the exuded metabolites are not yet identified. Further studies in this field may reveal which of these root metabolites plays the major role in the early stage of the initiation of the symbiotic relationship.

It becomes apparent that the information available on the factors which determine the initiation and the establishment of mycorrhizal symbiosis, has scratched only the surface of this complex problem and that there is an urgent need to intensify research in this field. The main emphasis in these studies should be placed on the relationship between the environment and the metabolites that are exuded by the roots and

by the fungus. Studies on root metabolites of herbaceous plants have provided evidence that the composition of root exudates differs under different environmental conditions (20, 31, 45, 72, 88). Similar differences may be expected in fungus exudates.

We can presume that under conditions which promote an accumulation of a surplus of soluble sugars in the tree roots, a factor which according to the carbohydrate theory assures the formation of mycorrhizae, root metabolites are produced and exuded in a composition which stimulates the hyphae of the fungal symbiont to grow towards and finally invade the roots. Similarly, we can presume that there are certain factors which stimulate the synthesis of auxin in the fungal hyphae. It has been reported that microorganisms convert certain amino acids, particularly tryptophane, into indoleacetic acid (83, 14).

It would be of great importance to know which factors determine the production of these auxins in the hyphae and under which conditions the fungus is able to produce auxin in the quantity necessary for optimum mycorrhizal development. Meanwhile, the possibility that, in addition to auxin, the fungus may supply other growth-promoting substances to the host plant (39, 43) emphasizes the need for extended investigations of the composition of fungus exudates.

Finally, it is important to know how in forest stands, in addition to climate and the physical and chemical factors of the soil, the complex population of soil microorganisms in the rhizosphere influences the formation of the mycorrhiza. Exact investigations in this field are only just beginning. However, evidence already has been obtained that the population of fungi is 15 to 20 times larger in the rhizosphere of oak seedlings with mycorrhizae than in the rhizosphere of seedlings lacking mycorrhizae (60). Moreover, in the rhizosphere of pine seedlings with mycorrhizae, a favorable bacterial flora of high nitrogen economy was found. Furthermore, in these experiments there was evidence of a close interrelation between the formation of mycorrhizae and *Azotobacter* (87). Seedlings of different tree species, inoculated with these bacteria, grew better and mycorrhizae were more abundantly formed.

In concluding this brief review about mycorrhiza and its significance to forest trees, it should be mentioned that it is difficult to find another problem in botany which has been beset by such confusion and so many contradictory opinions as mycorrhiza of forest trees. As already mentioned, there have been periods when the fungus was regarded as a harmful parasite. Skepticism about the benefit of mycorrhiza was expressed as recently as 1947 (62).

Although at present the significance of this symbiosis cannot be doubted, the opinion has been expressed that the significance of this association is overemphasized. Because of serious gaps in information, one can hardly accept or refute this statement. However, the fact cannot be overlooked that mycorrhiza is widespread and habitual among forest trees and that most of the feeding roots of forest trees are, as a rule, mycorrhizal. This means that most feeding roots of trees have lost their ability to absorb water and nutrient directly from the soil, since they lack root hairs and are isolated from direct contact with the soil by the hyphal mantle that surrounds them. Thus the gross supply of nutrient for the tree is provided by the fungus and the actual nutrient absorption from the soil is undertaken by the fungus hyphae.

Although it is generally accepted that mycorrhizal symbiosis is mutually beneficial, the fungus must be considered as an aggressor invading the roots in order to gain the maximum nutritional benefit from the host plant. According to Melin (50), mycorrhizal fungi may be considered primarily as parasites, since the fungi invade the host plant. He suggests, however, that unlike many real parasites, they do not seem, as a rule, to produce substances toxic to the host plant. The counter-action of root cells against the aggression of the fungus is clearly visible in sections of mycorrhizal roots examined under the microscope. However, the ability of the host plant to restrict the fungus invasion within certain limits does not assure an equilibrium in nutrient exchange between both associates.

Certain environmental conditions may change this equilibrium, and thus the symbiosis becomes more profitable for one of the associates. We can expect that, under conditions in which the fungus is favored in nutrient gain, the benefit for the tree through this symbiosis is far from optimum. That an association with mycorrhiza-forming fungi does not assure good growth of the tree, under certain environmental conditions, is convincingly illustrated in a picture published by Björkman (8). This picture depicts a 30-year old pine with well developed mycorrhizae. The height of the tree, however, is only 18 cm.

It is a fact that in vast areas still occupied by forests, the soil is usually deficient in certain nutrients. A good growth of trees in such soils can be achieved only through the aid of mycorrhizal symbiosis. Silviculturists must choose one or two approaches to this critical problem in forest biology. The symbiosis may be abandoned to the caprices of nature or, using knowledge that can be gained only from intensive research, it may be controlled so that the fungus, while obtaining a minimum profit from the association, will provide a maximum benefit for the tree.

Literature Cited

1. Alderich-Blake, R. N. 1930. Oxford Forest. Mem. 12: 1-60.
2. Andal, R., K. Bhuvaneswari, and N. S. Subba-Rao. 1956. Nature 178: 1063.
3. Anonymous. 1931. Rhodesia Agr. Jour. 28: 185-187.
4. Berbee, J. G. (Personal communication).
5. Bergemann, J. 1953. Mitteil. d. Bundesanstalt f. Forst- u. Holzwirts. 33: 77S.
6. _____. 1955. Zeits. f. Weltforstwirts. 5/6: 183-202.
7. Bhuvaneswari, K. and N. S. Subba-Rao. 1957. Proc. Indian Acad. Sci. 45: 299-301.
8. Björkman, E. 1942. Symb. Bot. Ups. 6: 1-190.
9. _____. 1944. Svensk Bot. Tidskr. 38: 1-14.
10. _____. 1949. Svensk Bot. Tidskr. 43: 223-262.
11. _____. 1956. Forstwissensch. Centralbl. 9/10: 265-286.
12. Börner, H. 1956. Beitr. zur Biol. der Pflanz. 33: 33-83.
13. Boullard, B. 1958. Bul. de la Soc. Bot. de France 105: 60-93.
14. Boysen Jensen, P. 1932. Biochem. Zeits. 250: 270-280.
15. Clowes, F. A. L. 1951. New Phytol. 50: 1-16.
16. Czapek, F. 1896. Jb. wiss. Bot. 29: 321-390.
17. Frank, A. B. 1885. Ber. dtsch. bot. Ges. 3: 27-33.
18. _____. 1885. Ber. dtsch. bot. Ges. 3: 125-145.
19. Frank, H. 1954. Planta 44: 319-340.
20. Frenzel, B. 1957. Planta 49: 210-234.
21. Fries, N., and B. Forsman. 1951. Physiol. Plant. 4: 410-420.
22. Gautheret, R. J. 1945. La culture des tissus. Gallimard. Ed. Paris, France, 1-202.
23. Harley, J. L. 1948. Biol. Rev. Cambridge Phil. Soc. 23: 127-158.
24. Harley, J. L. 1952. Ann. Rev. Microbiol. 6: 367-386.
25. _____ and J. K. Brierley. 1954. New Phytol. 53: 240-252.
26. _____ and C. C. McCready. 1950. New Phytol. 49: 388-397.
27. _____ and J. S. Waid. 1955. Plant and Soil 7: 96-112.
28. Hatch, A. B. 1936. Jour. Forestry 34: 22-29.
29. _____. 1937. Black Rock Forest Bul. 6: 1-168.
30. Hevesy, G. 1949. Ark. Bot. A 33. Stockholm.
31. Kandler, O. 1951. Zeits. Naturforsch. 6 b: 437-445.
32. Keller, H. G. 1952. Untersuchungen über das Wachstum von *Cenococcum graniforme* (Sow.) Ferd. et Winge auf verschiedenen Kohlenstoffquellen. Juris-Verlag. Zürich, Switzerland, 123 pp.
33. Kelley, A. P. 1950. Mycotrophy in plants. Chronica Botanica Co. of Waltham, Mass. New Ser. Plant Sci. Books 22: 1-223.
34. Kessell, S. L. 1927. Emp. Forest. Jour. 6: 70-74.
35. Kramer, P. J. and R. H. Hodgson. 1954. VIII^{e} Congres. Internat. de Bot. Sect. 13: 133-134. Paris.
36. _____ and K. M. Wilbur. 1949. Science 110: 8-9.
37. Kursanov, A. L. 1958. UNESCO/NS/RCI/128.
38. Levisohn I. 1952. Nature 169: 715.
39. _____. 1953. Nature 172: 316.
40. _____. 1957. The Emp. Forestry Rev. 36: 281-286.
41. Lindeberg, G. 1948. Physiol. Plant. 1: 196-205.
42. _____. 1955. Zeits. Pflanzenernähr. u. Bodenkunde 69: 142-150.
43. Lindquist, B. 1939. Bot. Notiser 1939: 315-356.
44. Lundegårdh, H. and G. Stenlid. 1944. Ark. Bot. A 31: 1-27. Stockholm.
45. Martin, P. 1956. Naturwiss. 43: 227-228.
46. McComb, A. L. 1938. Jour. Forestry 36: 1148.
47. _____. 1943. Bul. Idaho Agr. Expt. Sta. 314: 582.
48. Melin, E. 1925. Untersuchungen über die Bedeutung der Baummykorrhiza. Pp. 1-152. Jena, G. Fisher.
49. _____. Symb. Bot. Ups. 8: 1-116.
50. _____. 1953. Ann. Rev. Plant Physiol. 4: 325-346.
51. _____. 1954. Abstract, 8th Internat. Bot. Congr., Paris.
52. _____. 1954. Svensk Bot. Tidskr. 48: 86-94.
53. _____ and H. Nilsson. 1950. Physiol. Plant. 3: 88-92.
54. _____. 1952. Svensk Bot. Tidskr. 46: 281-285.
55. _____. 1953. Nature 171: 134.
56. _____. 1955. Svensk Bot. Tidskr. 49: 119-122.
57. _____. 1958. Bot. Notiser 111: 251-256.
58. _____ and E. Hacskaylo . 1958. Bot. Gaz. 119: 243-246.
59. Mikola, P. 1953. Karstenia II.
60. Misustin, E. N. 1951. Russ. Agrobiologija 2: 27.
61. Mitchell, H. L., R. F. Finn, and R. O. Rosendahl. 1937. Black Rock Forest Bul. 1: 58-73.
62. Möller, C. M. 1947. Forstl. ForsØqsv. i Danmark 19: 105-208.
63. Moser, M. 1956. Forstwiss. Centralbl. 1/2: 8-18.
64. Norkrans, B. 1950. Symb. Bot. Ups. 11: 1-126.
65. Oliveros, S. 1932. The Makiling Echo, Bur. of Forestry, Dept. Agr. Natural Res. of the Philippine Islands 11: 205-214.
66. Rayner, M. C. 1927. *Mycorrhiza.* An account of non-pathogenic infection by fungi in vascular plants and bryophytes. Wheldon & Wesley Ltd., London, England. Pp. 246.
67. Rees, T. 1958. Plant Physiol. 33 (supplement): 10.
68. Robertson, N. F. 1954. New Phytol. 53: 253-283.
69. Roeloffs, J. W. 1930. Boschbouwk. Tijdsch. Tectona 23: 875-907.

70. Romell, L. G. 1938. Svensk Bot. Tidskr. 32: 89-99.
71. Routien, J. D. and R. F. Dawson. 1943. Amer. Jour. Bot. 30: 440-451.
72. Schmidt, H. H. 1953. Ber. dtsch. bot. Ges. 66: 420-426.
73. Skoog, F. 1951. *Plant Growth Substances.* Pp. 1-476. Univ. Wisconsin Press.
74. Slankis, V. 1948. Physiol. Plant. 1: 390-400.
75. _____. 1949. Svensk Bot. Tidskr. 43: 403-707.
76. _____. 1950. Physiol. Plant. 3:40-44.
77. _____. 1951. Sym. Bot. Ups. 11: 1-63.
78. _____. 1955. Canad. Phytopath. Soc. Proc. 23: 20-21.
79. _____. 1958. In: *The Physiology of Forest Trees* (Symposium), K. V. Thimann (Ed.) Pp. 427-443. Ronald Press Co., New York.
80. _____. (Unpublished data).
81. _____. (Unpublished data).
82. _____, V. C. Runickles, and G. Krotkov. (In preparation).
83. Thimann, K. V. 1935. Jour. Biol. Chem. 109: 279-291.
84. _____. 1952. *The Action of Hormones in Plants and Invertebrates.* Pp. 1-228. Academic Press Inc., Publish., New York.
85. Timonin, M. I. 1941. Soil Sci. 52: 395.
86. Trappe, J. M. (Personal communication).
87. Tribunskaja, A. 1955. Russ. Mikrobiologija 24: 188-192. (Cited in Bergemann #5).
88. Virtanen, A. L. and S. V. Hausen, 1935. Nature 135: 184-185.
89. Vozujakovskaja, J. M. 1954. Russ. Mikrobiologija 23: 204-220. (Cited in Bergemann #5).
90. Wenger, K. F. 1955. Ecology 36: 518-520.
91. West, P. M. 1939. Nature 144: 1050-1051.
92. White, D. P. 1941. Ecology 22: 398-407.
93. Young, H. E. 1936. Jour. Austr. Inst. Agr. Sci. 2: 32-34.

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